

Cross-Sectional Morphology of the SK 82 and 97 Proximal Femora

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ABSTRACT Computed tomography scans of the proximal femoral shaft of the South African “robust” australopithecine, *A. robustus*, reveal a total morphological pattern that is similar to the specimen attributed to *A. boisei* in East Africa but unlike that of *Homo erectus* or modern human femora. Like femora attributed to *H. erectus*, SK 82 and 97 have very thick cortices, although they do not have the extreme increase in mediolateral buttressing that is so characteristic of *H. erectus*. And unlike *H. erectus* or modern humans, their femoral heads are very small relative to shaft strength. These features are consistent with both increased overall mechanical loading of the postcranial skeleton and a possibly slightly altered pattern of bipedal gait relative to that of *H. erectus* and modern humans. *Am J Phys Anthropol* 109:509–521, 1999. © 1999 Wiley-Liss, Inc.

Many studies have demonstrated the developmental plasticity and sensitivity of long bone diaphyses to applied mechanical loadings (Trinkaus et al., 1994, and references therein). It follows that the preserved diaphyseal morphology of skeletal or fossil remains should reflect, at least in part, the mechanical loadings to which it was subjected during life. The most mechanically relevant properties of a long bone diaphysis are its cross-sectional area and second moments of area, which are proportional to axial and bending/torsional rigidity, respectively (Lovejoy et al., 1976; Ruff and Hayes, 1983).¹ To calculate these properties, accurate reconstructions of both external (periosteal) and inter-

nal (endosteal) perimeters are necessary. A variety of techniques have been used to obtain these contours in modern and fossil long bones, including physical sectioning, use of natural breaks, multiplane radiography, and computed tomography (CT) (Ruff, 1989). In this study we report on the cross-sectional diaphyseal properties of the *Australopithecus robustus* SK 82 and 97 proximal femora as determined from CT scans.

The SK 82 and 97 specimens derive from Member 1 of Swartkrans, South Africa, and are dated to approximately 1.6–1.8 Myr (Vrba, 1985). They are attributed to the

¹These refer to the morphological (i.e., geometric) properties of bone. Bone strength and rigidity are dependent upon both morphological and material (e.g., tissue elasticity, ultimate stress) characteristics. Only morphological properties can be measured in fossils. However, there is evidence from experimental studies (reviewed in Ruff, 1989) that the major response of bone tissue to altered mechanical loadings is through geometric modeling/remodeling, rather than through changes in intrinsic tissue properties.

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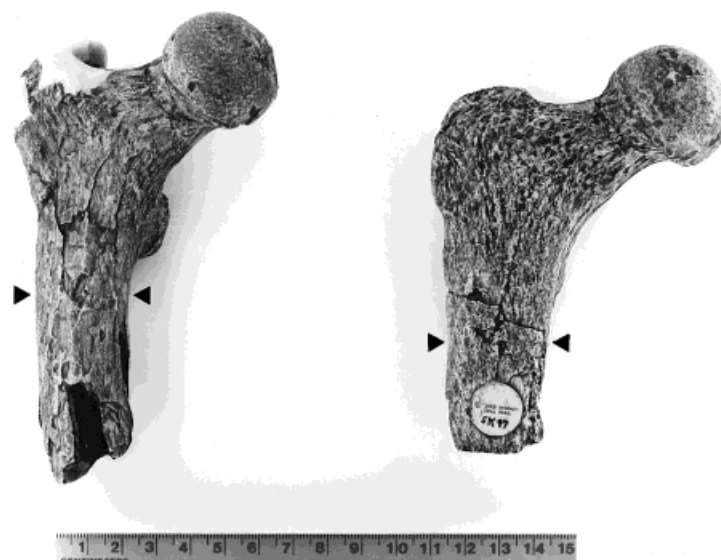


Fig. 1. Anterior views of casts of SK 82 (left) and SK 97 (right), with section locations indicated by arrowheads. Specimens positioned with head and neck in approximately 18° of anteversion (see text).

“robust” australopithecine taxon, *Australopithecus* (or *Paranthropus*; for discussion of terminology, see Strait et al., 1997; Skelton and McHenry, 1998) *robustus*, because over 95% of the taxonomically diagnostic craniodental material from that member can be attributed to that species (Grine, 1989), and also because of their non-*Homo*-like morphology (Napier, 1964; Robinson, 1972; McHenry, 1975c; Susman, 1989). They have figured prominently in discussions of the functional anatomy of the australopithecine lower limb (Napier, 1964; Day, 1969, 1973; Jenkins, 1972; Robinson, 1972; Lovejoy and Heiple, 1972; Lovejoy et al., 1973; Walker, 1973; McHenry, 1975a,c, 1994 and references therein; McHenry and Corruccini, 1976, 1978; Wood, 1976, 1978). Each specimen preserves the right femoral head, neck, trochanteric region, and several centimeters of the proximal shaft (Fig. 1), although parts of the greater trochanter and posterolateral shaft are reconstructed in SK 82 (Robinson, 1972). Together they preserve an excellent record of the *A. robustus* subtrochanteric diaphysis, an important skeletal region in assessing hip biomechanics (see references above; also Ruff, 1995, 1998).

METHODS

Each specimen was scanned at Johannesburg Hospital (Johannesburg, South Africa) using a Philips SR 7000 Tomoscan CT. Specimens were oriented with the longitudinal diaphyseal axis perpendicular to the scan plane, and the posterior surface of the head, greater trochanter, and shaft in contact with the scanning platform (thus, for scanning, the “mediolateral” axis was taken to be in the same plane as the head-neck, or cervical axis). Following a scout scan to determine the longitudinal position of bony landmarks, a series of 1.5-mm-thick slices at intervals of 1 cm were taken, beginning at the distal edge of the lesser trochanter and extending both proximally and distally from this position.

Slice images were displayed at a window width of 4,000 H and a window center of 1,185 H and made into hard copies.² These were then photographed on a light box and

²In practice, the images were adjusted on the CT viewing screen until they appeared sharp and stable. As noted below, dimensions of the images were very similar to those measured on the original specimens. These settings should not be taken as “standard” for any other analyses, however, since the most appropriate CT image window width and level will vary depending on the material composition of the specimen, the surrounding medium (e.g., air or water), and the machine employed for scanning (Ruff and Leo, 1986).

made into slides, which were rear-projected onto a digitizer, where endosteal and periosteal boundaries were manually traced. A modified version of the program SLICE (Nagurka and Hayes, 1980) was used to calculate section properties from x,y point coordinate data (see Ruff, 1989). Repeated tracings of the same sections yielded values for properties within 2%. The means obtained from three tracings of each section were used in the analysis.

Although several sections were analyzed in this way, results for only those lying 1 cm distal to the distal edge of the lesser trochanter are reported here (Fig. 1). This was done to allow comparisons with properties previously determined for other modern and fossil samples: in specimens of the same general size range as SK 82 and 97, the location used here approximates the "80% of femoral bone length" section included in other studies (Ruff and Hayes, 1983; Ruff, 1987a,b, 1995; Trinkaus and Ruff, 1989) (with "length" measured from the distal end of the femur to the superior surface of the femoral neck). The CT images of this section for SK 82 and 97 are shown in Figure 2. A chunk of antero-medial cortex in SK 82 appears to be slightly outwardly displaced (Fig. 2a), although comparisons with section images above and below this level indicate that the displacement is minimal; during tracing, contours were adjusted slightly to account for this. A portion of the posterolateral cortex in SK 97 (Fig. 2b) is fragmented or missing, but enough of the anterolateral and posterior cortices are preserved (together with parts of the posterolateral cortex itself) that endosteal and periosteal contours in this region can be reconstructed fairly accurately. Reconstruction was also aided through comparison with a slightly more proximal section of the same specimen, where the posterolateral cortex is better preserved. Comparisons of external A-P and M-L breadth dimensions, measured from the CT images and also measured directly on the original specimens, were within 0.5 mm.

In order to compare section properties of the SK 82 and 97 specimens with those of other hominid femora, it was first necessary to orient them within the same set of standardized global (i.e., whole bone) axes. In

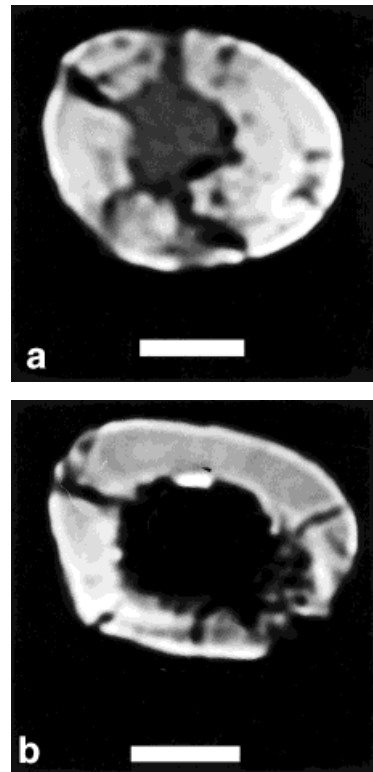


Fig. 2. CT scan images of (a) SK 82 and (b) SK 97, both taken transverse to the shaft at 1 cm distal to the distal edge of the lesser trochanter (see Fig. 1). Medial is at left, anterior is up. Section images are rotated clockwise (medial surface rotated anteriorly) by 18° to account for femoral neck anteversion, as described in the text. Mediollateral scale bars = 1 cm.

previous studies the mediollateral axis of the femur was taken to be parallel to the posterior surfaces of the femoral condyles (Ruff and Hayes, 1983). In specimens missing the distal femur, the linea aspera near midshaft may also be used to establish the anteroposterior axis. Neither of the Swartkrans proximal femora considered here are sufficiently complete to utilize these methods. However, a reasonable approximation of the correct diaphyseal orientation can be estimated from the preserved femoral head and neck of these specimens by assuming a particular anteversion angle, or deviation of the head-neck axis from the coronal plane of the shaft as established by the condylar axis.

It is clear from examination of all more complete earlier hominid femora, including those from australopithecines as well as

early *Homo* (e.g., KNM-ER 1472, 1481a, KNM-WT 15000g,h), that some degree of positive femoral anteversion (anterior projection of the head and neck) was present, as it is in most modern human femora (Yoshioka and Cooke, 1987). The anteversion angle of the *Australopithecus afarensis* AL 288-1 ("Lucy"), measured on a cast, is 18°. This is admittedly approximate, since the femoral condyles of this specimen were reconstructed. However, the posterior position of the linea aspera is consistent with this reconstruction, so this is very likely close to the true value. Two other possible australopithecine specimens from East Africa (KNM-ER 738 and 1463), from the same general time period as SK 82 and 97 (Feibel et al., 1989), preserve enough of the shaft and proximal femur so that an approximate anteversion angle can be estimated, using the linea aspera to establish the A-P axis. The value for KNM-ER 738 is about 17°, and that for KNM-ER 1463 about 22°, again measuring from casts. The latter value is more approximate, since KNM-ER 1463 is missing the femoral head. All three specimens are thus fairly consistent, with anteversion angles in the range of 17–22°. A value of 18°, based on the best preserved specimen (AL 288-1) but also between the other two, was therefore assumed for both SK 82 and 97. In practice, the mediolateral axis in section images was simply rotated by 18° prior to tracing on the digitizer.

The only section properties affected by this procedure are the angle of the major axis (orientation of greatest bending rigidity), and the A-P and M-L second moments of area (bending rigidities). While the assumption of a particular anteversion angle certainly carries some error, the effects on these section properties of varying the angle a few degrees in either direction are relatively small,³ and the error introduced is certainly smaller than that which would have resulted from assuming that no anteversion was present.

In the following analyses, structural properties of the SK 82 and 97 femora are

TABLE 1. Comparative fossil specimens

Specimen	Date (Myr) ¹	Previous taxonomic attribution	Reference ²
KNM-ER 1472	1.89	<i>Homo</i> sp.	6
KNM-ER 1481a	1.89	<i>Homo</i> sp.	6
KNM-ER 1808m,n	1.69	<i>Homo erectus</i>	10
KNM-ER 737	1.60	<i>Homo erectus</i>	4/12
KNM-ER 803a	1.53	<i>Homo erectus</i>	5/12
OH 28	~0.7	<i>Homo erectus</i>	2
KNM-ER 1500d	1.89	<i>Australopithecus boisei</i>	7, 11
KNM-ER 1503	1.89	<i>Australopithecus</i> sp.?	3, 7
KNM-ER 738	1.88	<i>Australopithecus</i> sp.?	8
KNM-ER 815	1.77	<i>Australopithecus</i> sp.?	9
OH 20	~1.7	<i>Australopithecus boisei</i> ?	1
KNM-ER 993	1.53	<i>Australopithecus</i> sp.?	9
KNM-ER 1463	1.53	<i>Australopithecus</i> sp.?	3, 7
KNM-ER 1465a	1.53	<i>Australopithecus</i> sp.?	3, 7

¹ Sources for dates: OH 20 and 28, Hay (1976); all others, Feibel et al. (1989).

² 1, Day (1969); 2, Day (1971); 3, Day (1976); 4, Day and Leakey (1973); 5, Day and Leakey (1974); 6, Day et al. (1975); 7, Day et al. (1976); 8, Leakey et al. (1972); 9, Leakey and Walker (1973); 10, Walker et al. (1982); 11, Grausz et al. (1988); 12, McHenry (1994).

compared with those of both modern humans (a pooled Amerindian-East African sample, $n = 100$) and other broadly contemporaneous fossil hominids from East Africa with available cross-sectional diaphyseal data from the same location on the femur ($n = 14$) (for details see Ruff, 1995). A list of the fossil specimens, their dates, previous taxonomic attributions, and references for these attributions is given in Table 1. Six of the East African specimens were previously attributed to *Homo* sp. or *H. erectus*, and eight to *Australopithecus*. However, only a few of these femora are associated with diagnostic cranial remains (or in the case of OH 28 derive from a time period where only one hominid species is represented), so that many taxonomic affinities are uncertain. This is particularly true for the two earliest *Homo* specimens (KNM-ER 1472 and 1481a) and all of the *Australopithecus* specimens except for KNM-ER 1500d. KNM-ER 1472 and 1481a share many similar morphological features with later *Homo erectus*, and have therefore often been considered to be "*Homo erectus*-like", if not actually *H. erectus* (or *H. ergaster*)⁴ (see McHenry, 1994; Ruff, 1995 and references therein). They contrast

³This was tested by tracing the SK 82 section at 18° of "anteversion" and at $\pm 5^\circ$ from this, i.e., at 13° and 23°. Resulting values for A-P and M-L second moments of area were within $\pm 3\%$ of their values at 18°. The angle of the major axis, of course, varied by $\pm 5^\circ$.

⁴Early (1.5–1.9 Myr) African *H. erectus* has been referred to as *H. ergaster* by some researchers (Wood and Collard, 1999). Therefore, this could include any of the *Homo* specimens listed in Table 1 except for the later OH 28. For present purposes, the two taxonomic designations will be considered synonymous.

TABLE 2. Section properties of SK 82 and 97¹

Specimen	Properties											
	CA	MA	TA	%CA	I _x	I _y	I _y /I _x	I _{max}	I _{min}	I _{max} /I _{min}	Theta	J
SK 82	490	87	577	84.9	21,637	31,261	1.445	31,992	20,907	1.530	165	52,899
SK 97	457	136	593	77.1	21,228	33,779	1.591	34,549	20,458	1.689	166	55,007

¹ CA, cortical area; MA, medullary area; TA, total periosteal area; %CA, [(CA/TA) · 100]; I_x, second moment of area about x (ML) axis (AP bending rigidity); I_y, second moment of area about y (AP) axis (ML bending rigidity); I_{max}, maximum second moment of area; I_{min}, minimum second moment of area; Theta, orientation of greatest bending rigidity (measured counterclockwise from lateral, as viewed from proximal end); J, polar second moment of area. Areas in mm², second moments of area in mm⁴, theta in degrees.

in morphology to that of *H. habilis* sensu stricto, as represented by OH 62, which had body proportions and femoral shaft characteristics more like those of *Australopithecus* (Johanson et al., 1987; Hartwig-Scherer and Martin, 1991). Because of this, it is not possible to definitively assign the non-*Homo* specimens (except for KNM-ER 1500d) in Table 1 to either *Australopithecus* or *Homo habilis* sensu stricto. For convenience in the following presentation and discussion of results, these specimens (and KNM-ER 1500d) will be referred to simply as “non-*H. erectus*,” while the six early *Homo* femora in Table 1 will be referred to as “early *H. erectus*.”

RESULTS

Section properties of the SK 82 and 97 diaphyses, measured 1 cm below the distal edge of the lesser trochanter, are given in Table 2. The two femora are quite similar in most respects, differing primarily in the relative thickness of the cortex: as also apparent in Figure 2, SK 82 has a relatively thicker cortex than SK 97. Quantified using the percent cortical area index ((CA/TA) · 100), SK 82 has an index of 84.9%, and SK 97, 77.1%. Relative to modern humans, both of these values are high. The mean percent cortical area (%CA) of the 100 modern femora is 62.3%, with a standard deviation of 7.3 and a total range of 44.5–78.7%. Even the thinner-walled SK 97 section has a higher %CA than all but two of the 100 modern specimens. Proximal shaft cortical area is plotted against total periosteal area in Figure 3 for the two Swartkrans specimens, the modern human sample, and the comparative fossil sample. All of the fossils fall above or in the upper half of the modern human distribution for CA relative to TA. The mean %CA of the 10 non-*H. erectus* femora (includ-

ing SK 82 and 97) is 75.5% (SD 8.2, range 61.3–87.8%) and for the six early *H. erectus* femora 75.4% (SD 7.1, range 65.1–84.5%), both of which are significantly higher than that for modern humans ($P < 0.001$, Tukey tests). Thus, on average, all earlier hominids have relatively thick proximal femoral cortices compared to modern humans. The same has been previously demonstrated throughout the femoral diaphysis of Pleistocene *Homo* (Ruff et al., 1993).

The magnitudes of second moments of area (measures of bending and torsional rigidity) and the ratios between second moments of area in perpendicular planes (i.e., I_y/I_x and I_{max}/I_{min}) are quite similar in SK 82 and SK 97, differing by 10% or less (Table 2). Thus, in terms of these biomechanically relevant “size” and “shape” parameters, the two specimens are very similar. Second moments of area can be converted to measures of cross-sectional *strength* (i.e., section moduli) rather than rigidity by taking them to the 0.73 power (Ruff, 1995). This has been done in Figure 4, which is a plot of proximal femoral shaft M-L bending strength against A-P bending strength for the same specimens shown in Figure 3. All but one of the non-*H. erectus* specimens, including SK 82 and 97, fall in the upper range of the modern human sample, i.e., they have relatively increased M-L vs. A-P bending strength. However, the increase in relative M-L bending strength of the proximal shaft is even greater in early *H. erectus* femora.

The strength of the proximal femoral shaft relative to femoral head size is another revealing functional/morphological characteristic that can be evaluated in SK 82 and 97. The sum of any two perpendicular second moments of area is equal to J, the polar second moment of area, which is proportional to torsional rigidity. Thus, J/2 can be

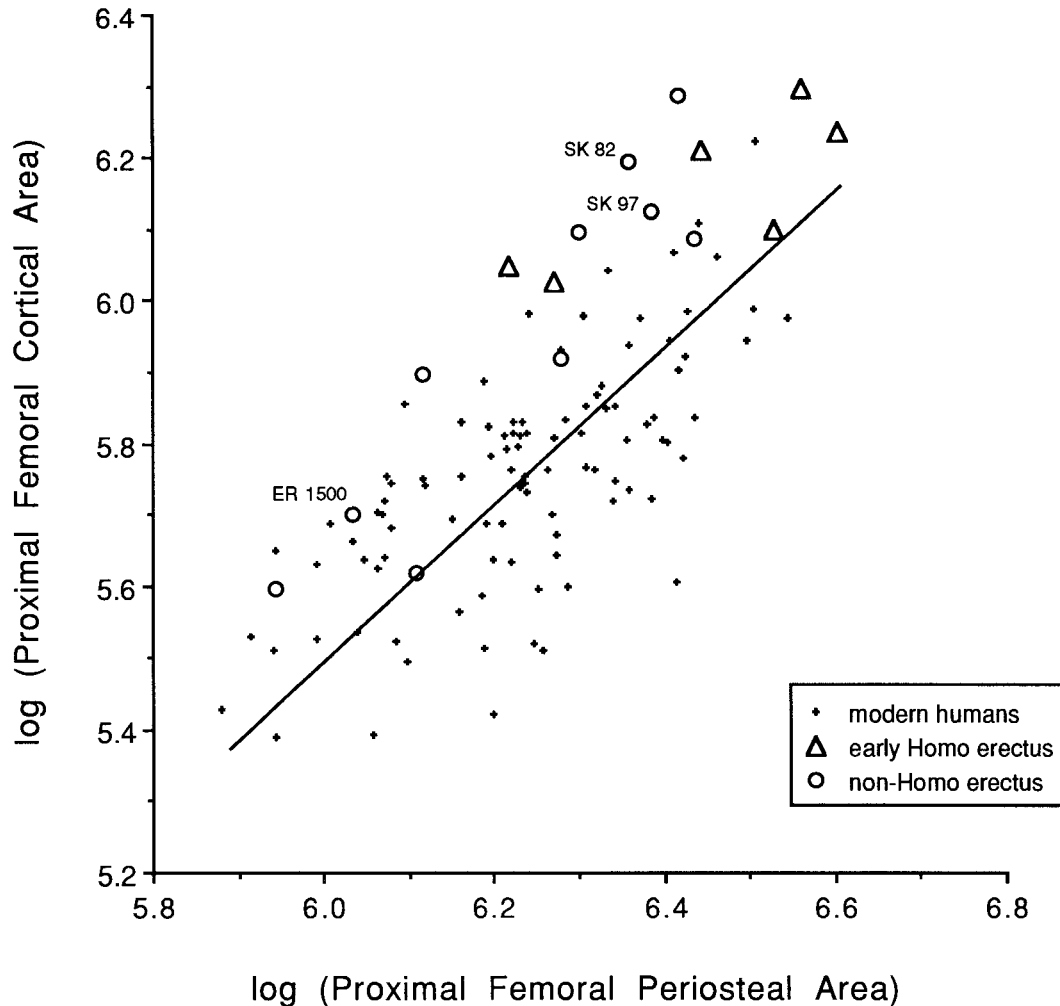


Fig. 3. Cortical area vs. total periosteal area of the femoral subtrochanteric shaft in modern humans (Pecos Pueblo Amerindians and East Africans), SK 82 and SK 97, and early *Homo erectus* and non-*H. erectus* East African specimens (see Table 1). Reduced major axis line plotted through modern humans. From smallest to

largest periosteal area, East African fossil specimens not attributed to *H. erectus* are KNM-ER 815, 1500d, 1463, 738, and 1503, OH 20, and KNM-ER 993 and 1465a; early *H. erectus* specimens are KNM-ER 1472, 1481a, and 1808n, OH 28, and KNM-ER 803a and 737 (KNM-ER 1808 restored as described in Ruff, 1995).

used as an index of both average bending rigidity and torsional rigidity (e.g., see Schaffler et al., 1985), which can be converted to an average equivalent strength measure by raising to the 0.73 power, as described above. This average strength measure is plotted against femoral head superoinferior breadth in Figure 5 for SK 82 and 97, the five other hominid fossils with available data, and the modern human sample. In addition, data for a sample of 43 African great apes (20 goril-

las, 20 common chimpanzees, and 3 pygmy chimpanzees) (Ruff, 1987b) are included for comparison.

SK 82 and 97, and the other two non-*H. erectus* specimens (KNM-ER 738 and 1503), are clearly quite different from modern humans in femoral shaft strength to femoral head size proportions (Fig. 5). As pointed out by previous researchers (Napier, 1964; Wood, 1976), their femoral heads appear very small relative to their proximal shafts when com-

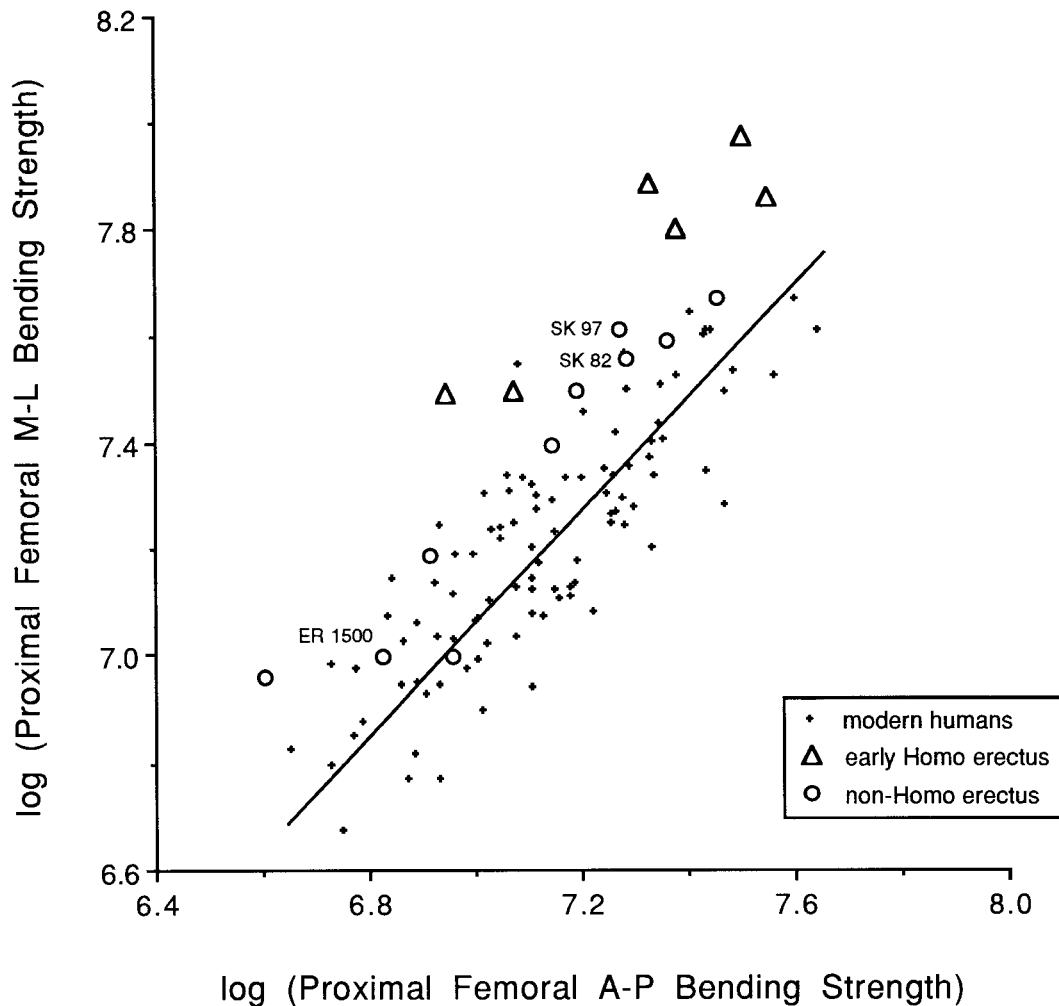


Fig. 4. Mediolateral vs. anteroposterior bending strength of the femoral subtrochanteric shaft in the same samples illustrated in Figure 3. Reduced major axis line plotted through modern humans. From smallest to largest A-P bending strength, East African fossil specimens not attributed to *H. erectus* are KNM-ER 815, 1500d, 1463, 738, and 1503, OH 20, and KNM-ER 1465a and 993; early *H. erectus* specimens are KNM-ER 1472 and 1481a, OH 28, and KNM-ER 1808n, 737, and 803a.

pared to modern humans. Interestingly, two of the three early *H. erectus* also have somewhat smaller femoral heads relative to proximal shafts than most modern humans. African apes have small femoral heads relative to shafts compared to modern humans, but are close in proportions to SK 82 and 97 (and the other two non-*H. erectus* specimens), as also noted previously (Napier, 1964).

DISCUSSION

In terms of cross-sectional biomechanical properties of the shaft, the SK 82 and 97

femora are very similar to each other, and to other non-*H. erectus* specimens from East Africa. Like all Plio-Pleistocene hominids, including *H. erectus*, they have relatively thick cortices (Lovejoy, 1982; Kennedy, 1985; Ruff et al., 1993). In terms of M-L strength of the shaft relative to A-P strength, they fall directly in line with East African *Australopithecus* (KNM-ER 1500d) and other non-*H. erectus* specimens, which as a group are distinctive from both modern humans and early *H. erectus*. Finally, their shaft strength relative to femoral head size is similar to

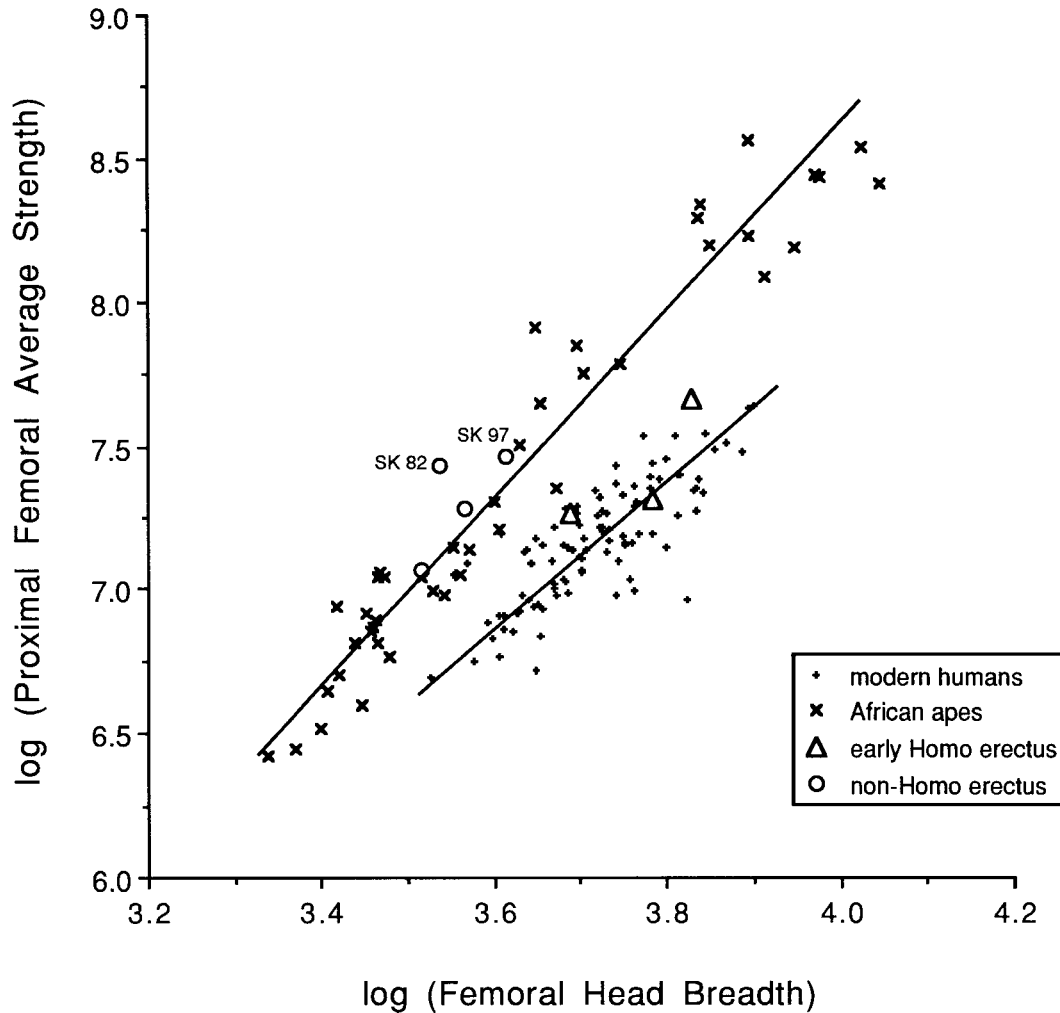


Fig. 5. Average bending/torsional strength of the femoral subtrochanteric shaft vs. femoral head breadth in modern humans (same sample as in Figs. 3 and 4), modern African apes, SK 82 and SK 97, and East African fossil hominid specimens. From smallest to largest femoral head breadth, East African specimens not attrib-

uted to *H. erectus* are KNM-ER 738 and 1503; early *H. erectus* specimens are KNM-ER 1472 and 1481a, and OH 28. African apes include 20 *Pan troglodytes*, 3 *Pan paniscus*, and 20 *Gorilla gorilla* (Ruff, 1987b). Reduced major axis lines plotted through both modern human and African ape samples.

that of other East African non-*H. erectus* specimens, and is again distinct from that of both modern humans and *H. erectus*.

At the least, this reinforces previous contentions that there is a group of proximal femoral specimens from East and South Africa that incorporate a homogeneous morphological pattern different from that of *Homo erectus* or modern humans (Day, 1969, 1973, 1976; Wood, 1976, 1978). SK 82 and 97 have been attributed to *Australopithecus*

robustus on taphonomic grounds, since over 95% of the craniodental remains from Member 1 of Swartkrans belong to that species (Grine, 1989). Only one East African specimen (KNM-ER 1500d) is associated with diagnostic mandibular material, and on this basis has been attributed to *A. boisei* (Grausz et al., 1988; but see Wood, 1991). Despite being much smaller in overall size, the morphology of KNM-ER 1500d is similar to that of the Swartkrans specimens (Figs. 3, 4). On

a purely morphological basis, then, the attribution of this specimen to *A. boisei* is supported by this analysis. In terms of overall size, i.e., magnitudes of cross-sectional areas and second moments of area, the Swartkrans femora are among the largest of the non-*H. erectus* specimens. They are most similar in both size and shape to KNM-ER 1465a, dated to 1.53 Myr, and OH 20, dated to about 1.7 Myr (Ruff, 1995), both of which are roughly contemporaneous with SK 82 and 97 (1.6–1.8 Myr).

Whether morphological similarity implies functional similarity is, of course, a more complex issue. One feature shared by almost all earlier hominid femora is an increase in M-L relative to A-P bending strength of the shaft compared to modern humans (Fig. 4; see also Ruff, 1995). Elsewhere, it has been shown that in modern humans this morphology is associated with increased femoral neck length relative to femoral length (Ruff, 1995). This would be predicted theoretically, since a long femoral neck displaces the diaphysis laterally from the hip joint, which should increase M-L bending moments in the shaft, especially proximally. Early *Homo erectus* have relatively long femoral necks (Ruff, 1995), which is one reason for the extreme M-L buttressing of their proximal femoral diaphyses (Fig. 4). *A. robustus* and *A. boisei* from South and East Africa have also been considered to possess relatively long femoral necks (Napier, 1964; Day, 1969; Walker, 1973; Wood, 1976), which could explain their relatively increased shaft M-L bending strength. While this appears to be a plausible explanation, it is difficult to evaluate without employing potentially circular reasoning, since there are no australopithecine femora from these taxa preserving both the neck and enough of the shaft to estimate femoral length with any precision, and other features that could be used as "size" indicators, such as femoral head size or proximal shaft breadth, are functionally related to neck length (Ruff, 1995). The composite reconstruction by Walker (1973) of an *Australopithecus* femur, based on East African specimens, gave a very long femoral neck relative to femoral length. The *A. afarensis* A.L. 288-1 ("Lucy") also has a long femoral neck relative to its length (see footnote 3 in

Ruff, 1995). Even these comparisons are complicated by the fact that lower limb length may have been substantially shorter relative to body size (mass) as a whole in at least *A. afarensis* (Ruff, 1991; Aiello, 1992; Franciscus and Holliday, 1992) if not *Australopithecus* generally (e.g., Sts 14; see Ruff, 1991). Thus, a high femoral neck/femoral length index in *Australopithecus* could be due in part to a relatively short femur.

Increased pelvic biacetabular breadth also leads to increased M-L bending of the femoral diaphysis, because of lateral displacement of the hip joint from the body center of gravity (Ruff, 1995). There are no pelvic specimens of *A. robustus* or *A. boisei* complete enough to estimate biacetabular breadth precisely. However, a general indication of the shape of the lower (true) pelvis can be gained from examination of the "iliac brim," or iliac portion of the linea terminalis. A relatively deeper (more curved) brim is associated with a more platypellic (M-L widened) pelvic inlet (Ruff, 1995). Two partial innominates from Swartkrans (SK 50 and the subadult SK 3155; Robinson, 1972; McHenry, 1975b) preserve enough of this region to allow measurement of the length (chord) and depth (subtense) of the iliac brim curve (for a more complete description and illustration of these measurements, see Ruff, 1995). The depth/length index in SK 50 is 0.184 and in SK 3155 is 0.174. The same index in a diverse sample of 89 modern humans averages 0.142, with a total range from 0.077–0.228 (Ruff, 1995). Because SK 3155 was not yet adult and because the pelvic inlet tends to increase more in M-L than in A-P breadth during adolescence (Moerman, 1981, our calculations), the somewhat lower index in SK 3155 may be due to its younger age. Taking the adult value of SK 50 as the more reliable of the two, an iliac brim index of 0.184 would indicate a moderately platypellic lower pelvis in *A. robustus* (predicted total pelvic inlet A-P/M-L ratio of 0.75, using a least squares regression on the modern human data shown in Fig. 16, Ruff, 1995), but not as extremely platypellic as the *A. afarensis* AL 288-1 (inlet A-P/M-L ratio of 0.58 (Tague and Lovejoy, 1986) or 0.67 (Häusler and Schmid, 1995)). The inlet shape of the *A. africanus*

Sts 14 is less certain, but appears to be moderately platypellic (inlet A-P/M-L ratio of 0.78 (Abitbol, 1995) or 0.88 (Häusler and Schmid, 1995)).

Thus, *A. robustus*, like other australopithecines, may have had a relatively M-L wide lower pelvis, which in turn would increase biacetabular breadth. If biacetabular breadth in robust australopithecines was at least not *small* relative to body size compared to modern humans, then a long femoral neck would result in a relative increase in M-L bending of the proximal femoral shaft (Ruff, 1995, 1998). This is, in fact, consistent with the morphology of the australopithecine (and other non-*H. erectus*) specimens examined here (Fig. 4). However, early *H. erectus* shows even more extreme M-L buttressing of the shaft (Fig. 4) (Ruff, 1995). Two possible explanations for this difference suggest themselves: 1) biacetabular breadth and/or femoral neck length were relatively larger in early *H. erectus* than in non-*H. erectus*, further increasing M-L bending of their femoral shafts, or 2) weight transmission through the non-*H. erectus* hip differed in a way that effectively reduced M-L bending of the femoral diaphysis relative to that of early *H. erectus*.

Without more complete specimens, the first possibility cannot be discounted, although on both theoretical and empirical grounds it seems unlikely (Ruff, 1991, 1995). The second alternative is supported by a biomechanical analysis of the more complete *Australopithecus afarensis* AL 288-1 pelvis and femur (Ruff, 1998). Specifically, if a theoretical "modern *Homo*-like" model of the hip (Ruff, 1995) is applied to AL 288-1, using her known pelvic and femoral dimensions, it predicts both a larger femoral head and an M-L stronger femoral shaft than she actually possessed in order to maintain biomechanical equilibrium (i.e., equivalent stresses under single-legged stance loading during bipedal gait). In contrast, the "modern *Homo*-like" model appears to work well in predicting the morphology of early *H. erectus* femora (Ruff, 1995). A possible explanation for this apparent discrepancy is that in contrast to modern humans (and *H. erectus*), AL 288-1's pelvis was tilted slightly upward on the nonsupport (swing) lower limb during bipe-

dal gait. This would have reduced both hip joint reaction and hip abductor forces on the support limb, which in turn would reduce M-L bending of the femoral shaft, consistent on all accounts with her observed morphology (Ruff, 1998). In the absence of more complete *A. robustus/boisei* specimens, we cannot know for sure whether the same explanation applies to these later australopithecines. However, given that all australopithecines appear to share the same general morphological features (apparently long femoral neck and wide biacetabular breadth, but only moderately increased M-L bending strength of the proximal diaphysis), the same model is at least consistent with the available morphological evidence. Whether this also applies to *H. habilis* *sensu stricto* will have to await more complete postcranial specimens definitively associated with this taxon.

Both the analysis of percent cortical area and average shaft bending/torsional strength vs. femoral head size suggest that *A. robustus* and *A. boisei* (KNM-ER 1500d) had a relatively very robust shaft (Figs. 3, 5), although to evaluate this precisely an independent measure of overall body size is needed (Ruff et al., 1993). Body mass in AL 288-1 can be estimated morphometrically, based on its preserved pelvis and estimated stature at about 27 kg, and relative to this body mass it has an extremely robust femoral shaft but average-sized femoral head when compared to modern humans (Ruff, 1998). If the same applies to other australopithecines, then SK 82 and 97 also had remarkably strong femoral shafts relative to body mass. There is also other independent evidence that robust australopithecines were actually small in overall body size (McHenry, 1991, 1992). Some isolated bones of the spine, foot, and hand of *A. robustus* match the size of their equivalents in a 28-kg modern human Pygmy, and most of the postcranial specimens are either equal to or smaller than their equivalents in a 45-kg modern Bantu skeleton. The entire *A. robustus* postcranial collection is composed of elements smaller in size than those in a 54-kg modern human except for dimensions of the femoral shaft.

As shown in Figure 5, modern humans have much weaker shafts relative to femoral head size than African apes, early *H. erectus* are slightly stronger on average than modern humans (see also Ruff et al., 1993), and non-*H. erectus* are much stronger than modern humans. Given that diaphyses are much more developmentally plastic in response to altered mechanical loadings than are articulations (Trinkaus et al., 1994; Churchill and Formicola, 1997), the most likely explanation for these findings is that relative to body mass, overall mechanical loadings of the skeleton are lowest in modern humans, were increased somewhat in early *H. erectus*, and were increased even more so in non-*H. erectus* (including SK 82 and 97), to about the same level as in modern African apes. This explanation appears reasonable in light of the known increased muscular strength of living apes relative to living humans (Bauman, 1926) and changing levels of cultural/technological sophistication (and thus decreasing reliance on physical strength vs. tools) during hominid evolution (Ruff et al., 1993). The slightly lower values for shaft strength/femoral head size in African apes compared to non-*H. erectus* indicated in Figure 5 may be due to the relatively large size of the femoral head in apes compared to other (nonhuman) primates, most likely related to increased joint excursion in apes (Ruff, 1988; Ruff and Runestad, 1992).

CONCLUSIONS

In terms of cross-sectional diaphyseal morphology, SK 82 and 97 are similar to the femoral specimen attributed to *Australopithecus boisei* as well as other non-*H. erectus* specimens from East Africa, and are distinct from both modern humans and early *H. erectus*. They share with early *H. erectus* the presence of relatively very thick cortices. They also exhibit increased mediolateral relative to anteroposterior bending strength of the proximal femoral shaft, although they are not as extreme in this regard as early *H. erectus*. Average shaft strength of *A. robustus* relative to femoral head size is greatly increased over that of modern humans, as well as early *H. erectus*, and is similar to that of extant African apes.

These results reinforce the impression of morphological continuity between *A. robustus* and *boisei*, and more generally, non-*H. erectus* femora from South and East Africa. To the extent that morphology reflects function, this may also indicate functional similarity in support of body mass and gait patterns. Without more complete specimens it is difficult to determine precisely how these patterns may have differed from those of early *H. erectus* and modern humans. However, the available morphological evidence indicates a generally increased level of mechanical loading of the skeleton in non-*H. erectus*, and is consistent with a slightly altered pattern of bipedal gait relative to that of modern humans and *H. erectus*.

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